

High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature

Zhenmin Lu, John W. Radin, Edgar L. Turcotte, Richard Percy and Eduardo Zeiger

Lu, Z.-M., Radin, J. W., Turcotte, E. L., Percy, R. and Zeiger, E. 1994. High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. – *Physiol. Plant.* 92: 266–272.

Advanced lines of Pima cotton (*Gossypium barbadense* L.) bred for higher yield potential and heat resistance have higher stomatal conductance and smaller leaf areas than those of obsolete lines. In controlled experiments, five commercial lines of Pima cotton having increasing lint yield and heat resistance showed a gradient of increasing stomatal conductance and decreasing leaf size. In field experiments, heat-sensitive, low yield Pima lines showed a lower stomatal conductance than high yielding, advanced lines. This indicates that selection for high yield potential and heat resistance has imposed a selection pressure for higher stomatal conductance and smaller leaf areas. The higher stomatal conductance and smaller leaf area in the advanced lines resulted in a lower leaf temperature in both controlled environments and in the field. The largest leaf temperature differences between obsolete and advanced lines were observed in the afternoon. These differences coincided with the largest differences in stomatal conductance and the highest air temperatures. Measurements of stomatal conductance and leaf temperature in field-grown progeny from a cross between the advanced line, Pima S-6, and the obsolete line, Pima 32, showed that genetically determined differences in stomatal conductance resulted in corresponding differences in leaf temperature. None of the altered physiological traits were selected for in the breeding program, indicating that selection for the desired agronomic traits imposed selection pressures on the altered physiological traits. The increases in stomatal conductance and decreases in leaf area could represent an integrated response to selection pressures on enhanced evaporative cooling, ensuing from selection for heat resistance.

Key words – Breeding, *Gossypium barbadense*, leaf area, leaf temperature, Pima cotton, stomatal conductance.

Z.-M. Lu and E. Zeiger (corresponding author), Dept of Biology, Univ. of California, Los Angeles, CA 90024, USA; J. W. Radin, USDA-ARS, Western Cotton Research Laboratory, Phoenix, AZ 85040, USA; E. L. Turcotte and R. Percy, Pima Cotton Breeding and Genetics, 37860 W. Smith-Enke Road, Maricopa, AZ 85239, USA.

Introduction

In the United States, Pima cotton (*Gossypium barbadense* L.) is grown primarily in the arid southwest, an area in which air temperatures $>40^{\circ}\text{C}$ are common throughout the growing season (Radin 1992). Breeding efforts at the USDA-ARS Maricopa Pima Improvement Project have been aimed primarily at improving lint quality and increasing yield potential, but breeding has also increased

resistance to high temperatures in each commercial release (Feaster and Turcotte 1962, 1984, Feaster et al. 1967, Niles and Feaster 1984). No attempts to modify physiological or morphological traits have been made in this program; instead, improvements have been achieved by genetic manipulation of available germplasm variability, extensive selection within segregating populations, and testing advanced generation lines for yield at sites with different temperature regimes.

Despite the lack of selection for physiological and morphological traits, a comparison between obsolete and advanced Pima lines shows that the extensive breeding has resulted in significant morphological and physiological changes. A greenhouse study of Pima lines differing in degree of selection has shown that photosynthetic rates and stomatal conductance increased in parallel with yield potential and heat resistance (Cornish et al. 1991). In the present study, we investigated possible selection pressures operating on stomatal properties and leaf size ensuing from the selection for higher yields and heat resistance, and their relationship with leaf cooling. The results show that leaves from advanced lines are cooler than those of obsolete lines under field conditions. The enhanced cooling would confer advanced Pima lines an avoidance type of heat resistance, which could be advantageous for growth and productivity in hot arid environments.

Abbreviations – gs, Stomatal conductance; LA, leaf area; Ta, air temperature; Tl, leaf temperature; VPD, vapor pressure difference.

Materials and methods

Plant material and genetic background

Four commercial lines of Pima cotton (*Gossypium barbadense* L.; Pima 32, Pima S-2, Pima S-3 and Pima S-6) and one elite strain (P70) were planted in a greenhouse and analyzed by steady-state gas exchange in the laboratory. Two heat-sensitive cultivars of *G. barbadense* (Sea Island and Morocco), one old (Pima 32) and one advanced (Pima S-6) commercial line, and five experimental elite strains (P67, P69, P71, P73 and P74) were planted and used in field experiments.

Sea Island, the oldest and most heat-sensitive cultivar used in the present study, is a late-maturing and low-yielding *G. barbadense* which was introduced into the southeastern US around 1785 (Stephens 1976). Morocco is another heat-sensitive *G. barbadense* commercially grown in Morocco. Pima 32 was developed from Egyptian and Sea Island germplasm in 1949, and represented an improvement in heat resistance and lint yield potential over Sea Island (Feaster and Turcotte 1962). Pima S-2 was released for commercial production in 1960, and it contains germplasm from Pima 32 (Feaster and Turcotte 1962). Yield increases of Pima S-2, relative to Pima 32, were attributed to earlier maturity and to enhanced heat resistance during the fruiting period (Feaster and Turcotte 1976). Pima S-3, released in 1966 as an alternative to Pima S-2 on less productive soils at high elevation (above 750 m), has germplasm from Pima S-1 and Pima 32 (Young et al. 1976). Pima S-6, released in 1983 as a replacement for Pima S-5, has germplasm from Pima 32 and Pima S-2 (Cornish et al. 1991). Pima S-6 is 35–60% more productive than Pima S-2, presumably because of increased earliness and improved heat resistance (Feaster and Turcotte 1984). The elite strain P70, given elite status

in the Pima Improvement Program in 1987, exhibits yields about 10% higher than Pima S-6 (E. Turcotte, unpublished observations). P69, a selection from a cross between Pima experimental strains related to Pima S-6, was commercially released in 1992 as Pima S-7. The yield of P69 averaged 10% more than Pima S-6 and its major advantages over Pima S-6 are earlier maturity and greater heat resistance (Turcotte et al. 1992). The genetic relations between these lines have been described in detail elsewhere (Cornish et al. 1991, Feaster and Turcotte 1962).

Greenhouse

Pima 32, Pima S-2, Pima S-3, Pima S-6 and P70 were grown in a UCLA greenhouse in Los Angeles for steady-state gas exchange measurements in 1990. Ten plants for each genotype were planted in 7.5-l pots with garden soil (Armstrong Potting Soil, Armstrong Garden Centers, Inc., Glendora, CA, USA). Plants were grown under natural sunlight (photosynthetically active radiation [PAR] 1600–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Air temperature was $30 \pm 3^\circ\text{C}$ and relative humidity (RH) was 40–50% during the day. Plants were irrigated daily and fertilized weekly (Spoonit [Yuba City, CA, USA] 18%N, 20%P, 16%K, 0.225% Fe).

Growth chamber

Pima S-6 and Pima 32 were planted and grown in a Conviron FGV36 growth chamber (Los Angeles Cascade, Van Nuys, CA, USA) for leaf temperature measurements. Growth space was $1.4 \times 2.4 \times 2.0$ m and plants were grown at a density of 6 plants m^{-2} . Plants were exposed to 12 h light/12 h darkness per day. Light fluence rates (incandescent: Philips [Philips Lighting Company, Somerset, NJ, USA], 40W, 120V; fluorescent: GTE [Sylvania, GTE Products Corporation, Winchester, KY, USA], F96T12/CW/VHO) were about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, air temperature was 42°C and RH was about 50%. During the dark period, temperature was 28°C and RH was 62%. Plants were watered twice daily in the morning and afternoon and fertilized twice a week.

Field

Field studies were conducted at the University of Arizona's Maricopa Agricultural Center, Maricopa, in 1991 and 1992. Sea Island, Morocco, Pima 32 and Pima S-6 were planted and grown in one field, and Pima S-6, P67, P69, P71, P73 and P74 were planted and grown in another field. The two fields were close to each other and had the same environmental conditions. All plants were grown under uniform soil conditions with the same irrigation and fertilizer treatments. Plants were well watered and fertilized throughout the growing season. The research fields were surrounded by a large area of cotton fields.

The genetic basis of the differences in stomatal conductance and leaf temperature between lines was studied in a cross between the advanced commercial line, Pima S-6, and the obsolete line, Pima 32. Both parents and their hybrids were planted and grown in the same field at the Maricopa Agricultural Center in 1993, in a randomized complete block design with five replicates.

Stomatal conductance

Stomatal conductance under controlled conditions was measured with a steady-state, gas exchange system (Armstrong Ent., Palo Alto, CA, USA) described by Zeiger et al. (1985). Light was provided by two GTE Sylvania projector lamps (500 W, 120 V), and measured with a Li-Cor quantum probe (Li-Cor, Inc., Lincoln, NE, USA). RH in the cuvette was controlled by a humidifier (Armstrong Ent.). Cuvette temperature was controlled electronically and measured with digital thermistors (Wescor, Inc., Logan, UT, USA) connected to a computer. Fully expanded leaves from the third or fourth node were used for all experiments. Measurements are the average of four plants obtained by enclosing a portion (25–30 cm²) of an intact, attached leaf into the gas exchange cuvette.

In the field and greenhouse, stomatal conductance was measured on the youngest fully expanded mainstem leaf from 10 plants of each line with a LI-1600 (Li-Cor) steady-state porometer.

Leaf and canopy temperature

Leaf temperatures were measured continuously with copper-constant thermocouples (Omega Engineering Inc., Stamford, CT, USA; model TT-T-40), attached to the underside of the leaves and connected to a CR21 Micrologger (Campbell Scientific, Inc., Logan, UT, USA). Air temperature was measured with a shaded thermocouple positioned 10–15 cm above the canopy. Leaf and air temperatures were measured with a thermocouple located inside the leaf chamber of the LI-1600 porometer. Canopy temperature was measured with an infrared thermometer (Everest Interscience, Inc., Los Altos, CA, USA, model 210) with a 4° field of view.

Leaf area

Leaf length and width were measured with a ruler. The dimensions were later converted to leaf areas from a regression relating the product of length and width to actual area ($r^2=0.83$). All measurements were conducted during the flowering and fruiting periods.

Statistics

Statistical analysis of the data was conducted by using SAS (1985). In all tables and figures, means followed by the same letter are not significantly ($P=0.05$) different,

as determined by Duncan's Least Significant Difference Test.

Results

Stomatal conductance

Gas exchange analysis showed that stomatal conductance in Pima lines increased in parallel with the increases in selection for lint yield. Stomatal conductance was lowest in Pima 32, the oldest line, and was highest in P70, the highest yielding elite line (Tab. 1).

Measurements of stomatal conductance in field-grown, obsolete and advanced lines of *G. barbadense* showed that the differences in stomatal conductance between Pima lines seen in the laboratory were also prevalent in the field. In one set of experiments we compared morning and afternoon conductance of the heat-sensitive cultivars, Sea Island and Morocco, the obsolete commercial line Pima 32, and the advanced, high-yielding line Pima S-6 (Fig. 1A). Morning conductance was higher than afternoon conductance in all lines, probably because of the higher vapor pressure differences (VPDs) and lower irradiances prevailing in the afternoon. Sea Island and Morocco leaves had the lowest stomatal conductance and Pima S-6 the highest. The obsolete line, Pima 32, showed a lower conductance than the advanced line Pima S-6, a finding consistent with the laboratory measurements. The largest conductance differences between lines were observed in the afternoon, during which air temperatures averaged 37°C.

Further testing of the hypothesis of a relationship between stomatal conductance and the extent of selection for higher yields and heat resistance was undertaken in field experiments comparing stomatal conductance in Pima S-6 with that of elite Pima lines. Elite lines are primary candidates for new commercial releases. To qualify as elite, lines had to show higher yield potentials and equal or greater heat resistance than Pima S-6, the commercial cultivar used until 1992. Consistently high stomatal conductance in the elite lines would therefore support the concept of a selection pressure for higher stomatal conductance ensuing from selection for heat

Tab. 1. Stomatal conductance and lint yield in obsolete and advanced Pima lines. Steady-state stomatal conductance was measured with a steady-state gas exchange system under controlled conditions: PAR = 1 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$, VPD = 0.5 kPa, $\text{CO}_2 = 350 \mu\text{l l}^{-1}$, $T_a = 30^\circ\text{C}$. Values are means of four replicates. Yields are averages obtained at Maricopa in 1990. Means within a column not followed by the same letter are significantly different at $P \leq 0.05$.

Line	gs ($\text{mol m}^{-2} \text{s}^{-1}$)	Lint yield (kg ha^{-1})
P70	0.74a	1 217
Pima S-6	0.70ab	984
Pima S-3	0.66b	707
Pima S-2	0.54c	856
Pima 32	0.58c	413

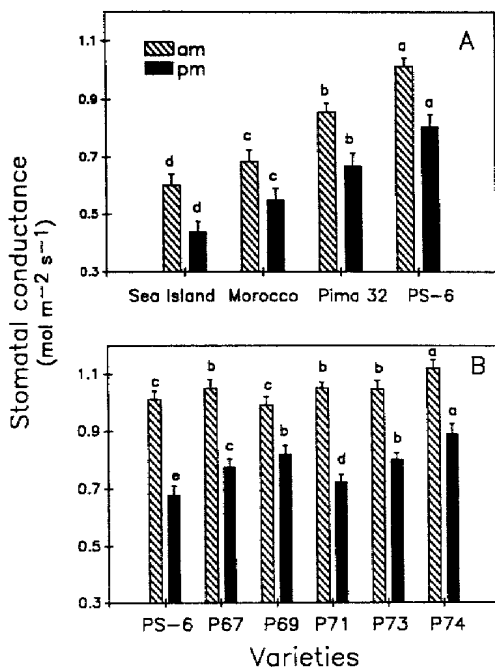


Fig. 1. Stomatal conductance in obsolete and advanced Pima lines grown in the field at Maricopa, Arizona. A. Conductance in the heat-sensitive lines, Sea Island and Morocco, the obsolete line, Pima 32, and the advanced line, Pima S-6. B. Conductance in the advanced line Pima S-6 and in experimental elite lines. Conductance measurements were obtained with a LI-1600 steady-state porometer. Young, fully expanded, mature leaves (3rd or 4th from the top of the canopy) were used in plants from all lines. Field conditions were: 11.00 h, PAR = 1750 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $T_a = 29^\circ\text{C}$, RH = 50%; 15.00 h, PAR = 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $T_a = 33^\circ\text{C}$, RH = 48%. Numbers are the average of 10 leaves; sd values are shown by vertical bars. Within the morning and afternoon data sets, bars not sharing the same letter represent values significantly different ($P \leq 0.05$) as determined by an analysis of variance.

resistance and higher yields. All elite lines had a stomatal conductance equal to or higher than S-6 (Fig. 1B). The trend toward higher conductance in the elite lines was more pronounced in the afternoon measurements, despite the lower absolute conductance values.

Leaf area

Advanced Pima lines also showed a significant decrease in leaf area under both greenhouse and field conditions (Tab. 2). As in the case of stomatal conductance, breeders did not use leaf area as a selection criterion (E. Turcotte, unpublished observations). This implies that selection for higher yield potential and heat resistance resulted in a selection pressure for smaller leaf areas. Plants from the same line grown in field and greenhouse conditions showed differences in leaf area, but obsolete lines had

Tab. 2. Single-leaf area (LA; cm^2) of obsolete and advanced Pima lines. In the field, all plants were grown in 1991 in the same environmental conditions at Maricopa. Measurements were obtained during the flowering and fruiting periods. Values are average leaf areas from 40 to 50 youngest, fully expanded 4th or 5th leaf from the top of the canopy. In the greenhouse, four leaves from each line were measured during the flowering time. Means not followed by the same letter are significantly different at $P \leq 0.05$.

Early heat-sensitive <i>G. barbadense</i>		Commercially released Pima lines		Experimental elite lines	
Lines	LA	Lines	LA	Lines	LA
<i>Field</i>					
Sea Island	233c	Pima 32	270a	P74	240b
Morocco	238c	Pima S-2	248b	P73	162d
		Pima S-6	166d	P70	159e
		Pima S-7 (P69)	157e		
<i>Greenhouse</i>					
		Pima 32	167a	P70	112e
		Pima S-2	170b		
		Pima S-3	157c		
		Pima S-6	120d		

larger single-leaf areas than advanced lines in both environments (Tab. 2).

Leaf temperature

Measurements of stomatal conductance and leaf temperature in the field showed that the two parameters were linearly related (Fig. 2). The higher stomatal conductance in advanced lines resulted in lower leaf temperatures, and the effect of stomatal conductance on leaf cooling was

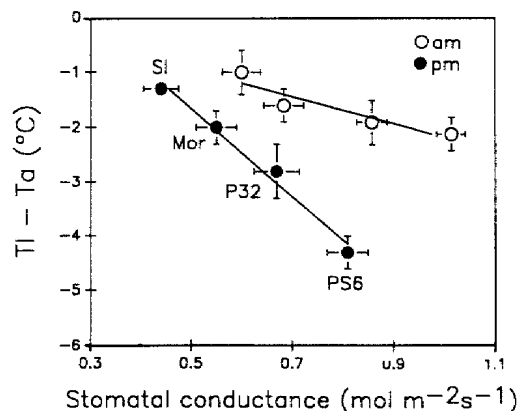


Fig. 2. Stomatal conductance and air-leaf temperature differences measured in the field. Stomatal conductance was measured as described in Fig. 1. Leaf and air temperatures were measured simultaneously with stomatal conductance. Values are means of 10 replicates. Bars represent sd values. The correlation coefficients between $T_l - T_a$ and stomatal conductance are significant at $P \leq 0.05$ for both morning (am) and afternoon (pm). SI, Sea Island; M, Morocco.

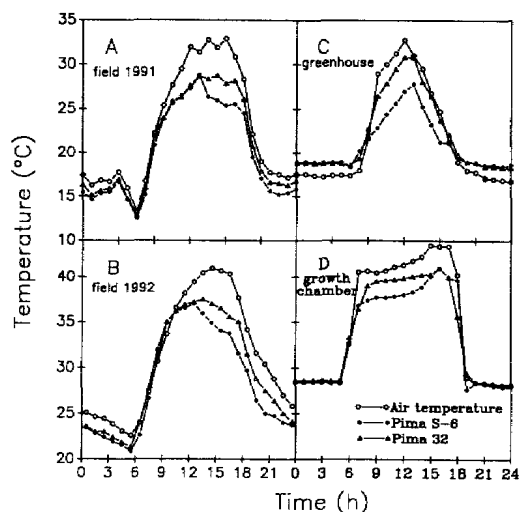


Fig. 3. Daily courses of air and leaf temperatures from leaves of the advanced line, Pima S-6, and the obsolete line, Pima 32. Measurements were conducted during the fruiting period in the field at Maricopa, Arizona (1991, A; 1992, B); in the greenhouse (C) and growth chamber (D) at UCLA, California in 1991. Both air and leaf temperature were measured with copper-constantan thermocouples. Data are the average of 3 leaves for (A), (C), (D) and 9 leaves for (B).

more pronounced in the afternoon than in the morning (Fig. 2).

The differences in leaf temperature between advanced and obsolete Pima lines were also observed in continuous measurements of air and leaf temperature under field, greenhouse and growth chamber conditions (Fig. 3). In the two sets of field measurements, one obtained in 1991 (Fig. 3A) and the other in 1992 (Fig. 3B), the largest temperature differences between the obsolete line Pima 32 and the advanced line Pima S-6 were observed in the afternoon, coinciding with the largest observed differences in stomatal conductance.

The differences in stomatal conductance between lines

Tab. 3. Canopy temperature (T_c , °C) in obsolete and advanced lines. Canopy temperature was measured in the field with an infrared thermometer in parallel with the stomatal conductance measurements. Values are the average of four measurements obtained on 4 different days. Field conditions during the measurements were: am, $T_a = 34^\circ\text{C}$, $\text{RH} = 44\%$, $\text{PAR} = 1700 \mu\text{mol m}^{-2} \text{s}^{-1}$; pm, $T_a = 36^\circ\text{C}$, $\text{RH} = 38\%$, $\text{PAR} = 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. Plants were well watered throughout the measurements. Means within a column not followed by the same letter are significantly different at $P \leq 0.05$.

Lines	T_c	
	am	pm
Sea Island	29.2a	33.3a
Pima 32	28.6b	32.4b
P70	28.9b	30.3c

also resulted in a difference in plant canopy temperature. The advanced line P70 had a canopy temperature that was about 3°C cooler than the canopy temperature of the heat-sensitive cultivar, Sea Island (Tab. 3). The canopy temperature differences were also more pronounced in the afternoon than in the morning.

Genetic basis of the differences in stomatal conductance and leaf temperature

Measurements of stomatal conductance and leaf temperature in field-grown progeny from a cross between the advanced line, Pima S-6, and the obsolete line, Pima 32, showed that the differences in stomatal conductance and leaf temperatures were genetically determined (Tab. 4). The relationship between stomatal conductance and leaf temperature indicates that selection pressures on cooler leaves would generate selection pressures on higher stomatal conductance.

Discussion

The results indicate that selection for higher yield potential and heat resistance in Pima cotton has generated lines having genetically determined, higher stomatal conduct-

Tab. 4. Genetic basis of the difference in stomatal conductance and leaf temperature in obsolete and advanced Pima lines. The parental lines (P) Pima S-6 and Pima 32 and their hybrids (F_1 , F_2 , BC1) were grown in the field at Maricopa in 1992. Stomatal conductance and leaf temperature were measured with a LI-1600 steady-state porometer in the afternoon during the month of July. Plants were at the flowering stage. Conditions during measurements were: $T_a = 37^\circ\text{C}$; $\text{PAR} = 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$; $\text{RH} = 38\%$. gs, Stomatal conductance; TI- T_a , difference between leaf and air temperature; F_1 , first generation; F_2 , second generation; BC1, back cross; n, number of plants. Means within a column not followed by the same letter are significantly different at $P \leq 0.05$.

Generation	gs ($\text{mol m}^{-2} \text{s}^{-1}$)	TI- T_a ($^\circ\text{C}$)	gs ($\text{mol m}^{-2} \text{s}^{-1}$)	TI- T_a ($^\circ\text{C}$)	n
Pima S-6			Pima 32		
P	$0.88 \pm 0.09a$	$-4.0 \pm 0.5a$	$0.46 \pm 0.06b$	$-1.1 \pm 0.3c$	20
Pima S-6 (φ) \times Pima 32			Pima 32 (φ) \times Pima S-6		
F_1	$0.64 \pm 0.10c$	$-3.5 \pm 0.7b$	$0.49 \pm 0.10b$	$2.1 \pm 0.4b$	20
F_2	$0.58 \pm 0.18d$	$-2.4 \pm 0.9c$	$0.62 \pm 0.20a$	$-2.6 \pm 1.1ab$	45
BC1	$0.71 \pm 0.10b$	$-3.7 \pm 0.9ab$	$0.49 \pm 0.10b$	$-2.8 \pm 0.7a$	35

ance and smaller leaf areas. Since neither of these traits has been selected for (E. Turcotte, unpublished observations), these physiological properties have probably been modified by selection pressures ensuing from selection for desired agronomic traits. Characterization of the functional relationship between the altered traits and the attained higher yield and enhanced heat resistance should facilitate the use of physiological traits as selection criteria.

The data show that stomatal conductance in advanced Pima lines is consistently higher than that of obsolete lines in different environments. This is the first report on a historical series of a cultivated species encompassing 40 years of selection that shows stable increases in conductance associated with higher yields. These findings indicate that the increases in stomatal conductance could be causally related to the increases in yield. Such causal relationship is supported by the finding that all high-yielding elite lines tested have high stomatal conductance, and by a similar relationship between higher stomatal conductance and higher yield potential found in bread wheat (D. Rees, Z. Lu, T. Nava, E. Acevedo and E. Zeiger, unpublished data). Evidence for an effect of selection on stomatal conductance per se, as opposed to changes in stomatal conductance mediated by effects of selection on other factors such as photosynthetic rates (Cornish et al. 1991), includes the findings that stomatal conductances in both a heat-sensitive, low conductance line, and a heat-resistant, high conductance line growing in the field were substantially higher than the threshold conductances imposing stomatal limitations on photosynthesis (Radin et al. 1994). In addition, specific physiological properties of guard cells, such as temperature sensitivity, the magnitude of their response to blue light, and their respiration and proton pumping rates, have also been altered by the selection process (Z. Lu and E. Zeiger, unpublished data; Quiñones et al. 1993, Srivastava and Zeiger 1991).

Selection for heat resistance might have favored genotypes having an enhanced evaporative cooling and lower leaf temperature mediated by higher stomatal conductance. Pima cotton is typically grown under high irradiance, high temperatures and abundant water supply, and these conditions favor rapid growth, early ground cover and high productivity. Stress resistance, however, can be readily exceeded under high irradiance and temperatures. Optimal daytime growth temperatures for cotton are substantially lower (29–32°C; Burke et al. 1988, Reddy et al. 1992) than prevailing maximal air temperatures in the southwestern United States during the growing season (>40°C; Radin 1992). In addition to deleterious effect on growth and biomass production, high temperatures also hinder pollination and fruit setting (Carns and Mauney 1968). Cooler leaves appear to have provided advanced Pima lines with a heat avoidance mechanism, which favors higher yield potential (Radin et al. 1994). Since Pima cotton grown in the Southwest receives ample water supply by irrigation throughout its growing season,

the advantage of an enhanced evaporative cooling achieved by high transpiration rates does not entail a risk of water stress. It is of interest that these breeding and growing conditions are also typical of the bread wheat grown in midwestern Mexico, which shows a pattern of physiological changes similar to that found in cotton (D. Rees, Z. Lu, T. Nava, E. Zeiger and E. Acevedo, unpublished data).

The prevalence of selection pressures for cooler leaves is consistent with the observation that the largest leaf temperature differences between advanced and obsolete lines were measured in the afternoon, at which time maximal daily air temperatures usually occur. In addition, leaves of advanced lines were cooler than those of obsolete lines under different growing conditions.

The measured leaf temperature differences between obsolete and advanced lines are not large enough to account for prevailing differences in yield potential on the basis of the temperature-dependent increases in biomass production measured in one Pima line (Reddy et al. 1992). On the other hand, enhanced leaf cooling could maintain leaf temperatures within an adaptive 'window' (Burke et al. 1988) which would prevent the triggering of heat-stress signals in the leaf. Heat stress in Pima cotton has a strong effect on flower bud (squares) production and retention (Reddy et al. 1992). If square production and retention is controlled in part by leaf processes having a strong temperature dependence, leaf cooling could improve yields. A detailed investigation of the effect of leaf temperature on square production and retention could prove rewarding.

The functional relationship between smaller leaf areas and higher yield potential and heat resistance is also of interest. Boundary layer resistance and heat transfer are markedly dependent on leaf dimensions (Nobel 1991). In natural populations growing under high temperatures and a limited water supply, a reduction in leaf size is beneficial to the plant because it lowers boundary layer resistance and increases heat dissipation (Taiz and Zeiger 1991). Leaves of irrigated cotton, however, have high transpiration rates and temperatures substantially below ambient air. Use of the energy balance model to simulate the effect of leaf width on leaf temperature at high irradiance and high stomatal conductance showed that leaf temperature decreases with width (Lu et al. 1992; Z. Lu and E. Zeiger, unpublished data). Thus, the smaller leaf area of the advanced Pima lines might contribute to their enhanced heat resistance.

It is of interest that leaves from the more productive upland cotton are smaller than leaves from Pima S-7, the commercial Pima line currently in use (Z. Lu, unpublished observations). In contrast with stomatal conductance, which was uniformly high in all elite lines (Fig. 1B), the elite line P74 had a large single-leaf area typical of obsolete lines (Tab. 2). This observation suggests that selection pressures for higher stomatal conductance have been stronger than those for leaf area. On the other hand, the elite line P69 (Fig. 1B), released as the newest com-

mercial line, Pima S-7 in 1992, has a single leaf area significantly smaller than that of the previous commercial release, Pima S-6 (Tab. 2). This relationship is consistent with the trend toward smaller leaf areas seen in the selection gradient.

The increases in stomatal conductance and the decrease in leaf area found in advanced lines of Pima cotton might represent an integrated response to selection pressures for enhanced evaporative cooling. Explicit selection for these physiological traits could result in further increases in heat resistance and yield potential.

Acknowledgments – The authors thank Mr M. Hu for assisting with the statistical analysis. This research was funded by Grant 91-03070 from the USDA Competitive Research Grants Office to E.Z.

References

- Burke, J.J., Mahan, J.R. & Hatfield, J.L. 1988. Crop-specific thermal kinetic windows in relation to wheat and cotton biomass production. – *Agron. J.* 80: 553–556.
- Carns, H.R. & Mauney, J.R. 1968. Physiology of the cotton plant. – In *Cotton* (F.C. Elliot, M. Hoover and W.K. Porter, Jr, eds), pp. 41–73. Iowa State Univ, Ames, IA.
- Cornish, K., Radin, J.W., Turcotte, E.L., Lu, Z.-M. & Zeiger, E. 1991. Enhanced photosynthesis and stomatal conductance of Pima cotton (*Gossypium barbadense* L.) bred for increased yield. – *Plant Physiol.* 97: 484–489.
- Feaster, C.V. & Turcotte, E.L. 1962. Genetic basis for varietal improvement of Pima cottons. – USDA-ARS, pp. 34–90.
- & Turcotte, E.L. 1976. Registration of Pima S-2 cotton. – *Crop Sci.* 16: 603.
- & Turcotte, E.L. 1984. Registration of Pima S-6 cotton. – *Crop Sci.* 24: 382.
- , Turcotte, E.L. & Young, E.F. 1967. Pima cotton varieties for low and high elevations. – USDA-ARS, pp. 34–90.
- Lu, Z.-M., Chen, J.-W., Radin, J.W., Percy, R., Turcotte, E.L. & Zeiger, E. 1992. Roles of stomatal conductance and leaf size in the regulation of leaf temperature in Pima cotton (*Gossypium barbadense* L.). – *Plant Physiol.* 99: S11.
- Niles, G.A. & Feaster, C.V. 1984. Breeding. – In *Cotton* (R.J. Kohel and C.F. Lewis, eds), pp. 201–231. Madison, WI. ISBN 0-89118-077-X.
- Nobel, P.S. 1991. *Physicochemical and Environmental Plant Physiology*. – Academic Press, San Diego, CA. pp. 354–367. ISBN 0-12-520020-X.
- Quiñones, M.A., Lu, Z.-M. & Zeiger, E. 1993. Zeaxanthin concentrations co-segregate with the magnitude of the blue light response of adaxial guard cells and leaf stomatal conductance in an F_2 population of Pima cotton. – *Plant Physiol.* 102: S15.
- Radin, J.W. 1992. Reconciling water-use efficiency of cotton in field and laboratory. – *Crop Sci.* 32: 13–18.
- , Lu, Z.-M., Percy, R.G. & Zeiger, E. 1994. Genetic variability for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. – *Proc. Natl. Acad. Sci. USA*. (In press).
- Reddy, K.R., Hodges, H.F., McKinion, J.M. & Wall, G.W. 1992. Temperature effects on Pima cotton growth and development. – *Agron. J.* 84: 237–243.
- SAS Institute. 1985. *SAS User's Guide: Statistics*. SAS Inst., Cary, NC. ISBN 0-917382-66-8.
- Srivastava, A. & Zeiger, E. 1991. Guard cells from advanced lines of Pima cotton (*Gossypium barbadense* L.) selected for high yield and heat resistance have enhanced rates of respiration and proton pumping. – *Plant Physiol.* 96: 5–30.
- Stephens, S.G. 1976. The origin of Sea Island cotton. – *Agric. Hist.* 50: 391–399.
- Taiz, L. & Zeiger, E. 1991. *Plant Physiology*. – Benjamin/Cummings, Redwood City, CA., pp. 90–93. ISBN 0-8053-0153-4.
- Turcotte, E.L., Percy, R.G. & Feaster, C.V. 1992. Registration of 'Pima S-7' American Pima cotton. – *Crop Sci.* 32: 1291.
- Young, E.F., Feaster, C.V. & Turcotte, E.L. 1976. Registration of Pima S-3 cotton. – *Crop Sci.* 16: 604.
- Zeiger, E., Iino, M. & Ogawa, T. 1985. The blue light response of stomata: pulse kinetics and some mechanistic implications. – *Photochem. Photobiol.* 42: 759–763.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.